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Continent-wide test of the efficiency of the European union's conservation legislation in delivering population benefits for bird species



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ABSTRACT

Birds are among the most important organisms for indicating the state of environmental health and their population changes may be thus informative for assessments of country-level conservation tools. One such tool applied in the European Union (EU) is the Birds Directive which (together with general protection of all bird species) lists a number of species under its Annex I and these species enjoy specific protection conditions. Although some previous studies found indications of the efficiency of the Annex I in delivering benefits for the listed species, the assessments were either confined to the so called old member states (i.e. countries entered EU before 2004) or did not include countries outside EU as a suitable control group. Therefore, it remains unclear whether this tool is efficient also in the new EU-member states (i.e. countries entered EU from 2004 onwards). For this purpose, we used publicly available information source and assembled a dataset providing country-level population trends of 252 European breeding bird species estimated for the time period 2001–2012 in 33 European countries containing old member states, new member states and non-member states. We predicted that if efficient, then listing the species under Annex I would result in significantly positive population trends of the listed species in EU countries irrespective to the time of their entrance, while no such pattern should be observed in non-EU countries. We tested this prediction using linear mixed effect models controlling for the effects of 11 species' traits reflecting the influence of other factors (e.g. climate change, land cover change, proximity to range edges) on trends and including the species and country identifiers as random effects. We found that the listing under the Annex I had significantly positive effect on bird trends in both old and new member states, whereas no such effect was observed in the non-member states. Although the positive influence of listing was larger in the old and than in the new member states, the difference was not statistically significant. Our results imply that the Annex I of the Birds Directive is an important tool for bird conservation in Europe and that its positive influence on bird populations is detectable even in the new EU members entering EU relatively recently. As birds are often used as indicators also for other groups of organisms, these results suggest that not only birds may benefit from EU's conservation legislation but comprehensive assessments are needed.

1. Introduction

Due to their generally large body size, diurnal activity and popularity among citizen scientists (Jiguet et al., 2012; Morelli et al., 2014), birds play a major role in indicating efficiency of conservation actions (Butchart et al., 2010). For instance, annual changes in population size of farmland birds were used to develop the Farmland Bird Index (Gregory et al., 2005), which is included among official indicators of environmental health in the European Union (EU). As indicators, populations of bird species mirror influences of factors acting at larger spatial scales (Gregory and van Strien, 2010) and their population changes may be thus informative for assessment of country-level conservation tools.

One of such conservation tools applied at the country level is legal protection of endangered species (McCarthy et al., 2012). By that means, species with unfavourable population status may be listed as protected in a given country and specific regulations (e.g. prohibition of their hunting and disturbance of individuals, restrictions to alteration of their habitats, direct support of impoverished populations) are agreed as the measures aiming to improve their populations (Vorisek et al., 2008). If efficient, population trends of species being listed as legally protected should be more positive than the trends of the species for which no such tool was developed (Koleček et al., 2014), although a time lag may exist between the time of listing and detectable population improvement (Male and Bean, 2005).

In EU, legal protection of birds is applied through the Birds

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Directive which states general conditions for protection of all bird species on the territory of EU-member countries (Council Directive 79/409/EC on the conservation of wild birds). In addition, the Birds Directive also lists a number of species under its Annex I and these species enjoy specific protection conditions, most notably manifested by establishment of Special Protected Areas (SPAs) conserving key sites for these species in individual countries (Donald et al., 2007). Such a combination of species- and area-focused protection may be a particularly powerful tool for conserving of animal populations (Sutherland, 2000) and, for that reason, it deserved high attention from the side of researchers testing its efficiency (e.g. Donald et al., 2007; Pellissier et al., 2013; Sanderson et al., 2016; Gamero et al., 2017). Specifically, they tested whether species listed under Annex I really benefited from their listing, i.e. whether it resulted in significant improvement of their population status.

These previous studies found that the listing of the species under the Annex I of the Birds Directive contributes significantly to their population increase (Donald et al., 2007; Gamero et al., 2017) and that the population improvement was larger with the longer the time since listing (Sanderson et al., 2016). However, the previous tests also showed a great difference between the old and new EU-member states (i.e. the states that entered EU before 2004 and the states entered from 2004 onwards, respectively) when the significant improvement was found only in the old members, but not in the new members (Sanderson et al., 2016). This finding thus poses an important question, whether the efficiency of this legislative tool for bird conservation is confined specifically to some selected countries being part of European democratic structures for considerably long time, while it may fail to provide conservation benefits in the new member states which underwent different historical development, as some studies already showed that these historical differences mirror in bird population changes (Reif et al., 2011; Koleček et al., 2015).

To fill this knowledge gap, our study, for the first time, assembled publicly available data on bird population trends from 2000 to 2012 in 33 European countries of a continent-wide coverage including the states in the Eastern part of Europe (e.g. Russia, Belarus and Ukraine) whose bird populations have almost been neglected up to now. This set of countries includes (i) the states entering EU before 2004 (i.e. the ‘old member states’ or EU-15), (ii) the states entering EU from 2004 or onwards (the ‘new member states’) and (iii) the states being non-members of EU. Such a design provides a strong test for the impact of listing the species under the Annex I assuming that the population trends estimated over the focal time period were affected by the entrance of a given country into the EU.

In this context, we tested two predictions. (i) If this legislative tool was efficient, then listing the species under Annex I would result in significantly positive population trends of the listed species in the EU member states irrespective to the time of their entrance, while no such pattern should be observed in the non-member states. (ii) If the time since listing matters, we predict that the population trends of the listed species should be more positive in the old member states than in the new member states.

In addition to the effect of legal protection, interspecific variability in population trends is influenced by various other factors including land use change, climate change or proximity to range edge (e.g. Devictor et al., 2012; Cuervo and Møller, 2013; Diaz et al., 2015). Their influence may be quantified by the relationships between the trends and species-specific traits reflecting the effects of particular environmental filters thereby a group of species sharing a given trait should exhibit similar population trends (Webb et al., 2010). Therefore, we considered the species’ traits recently recognized by a review of Reif (2013) as important predictors of bird population trends and accounted for their effects in the analysis (see Table 1 for the expected relationships and their justifications).

2. Materials and methods

2.1. Population trends

We focused on 252 bird species breeding in Europe that were previously analysed for potential range shifts by Koschová et al. (2014), see Supplementary Table S.1. We excerpted their national population trends for 33 European countries (Supplementary Table S.2) over the time period from 2001 to 2012 from the European Red List of Birds (BirdLife International, 2015). Because not all species breed in every country, we finally obtained the dataset with 4459 species-country combinations. These trends were expressed as relative change over the focal time period in per cent when negative percentage values quantified population declines, whereas positive percentage values quantified population increases (BirdLife International, 2015). When the trend was provided as a range of the maximum and minimum estimates (e.g. decline from -30% to -60%), we calculated the mean trend from these values (i.e. -45%). Quantification of population change as percentage raises concerns about comparability of the magnitude of change between declining and increasing species since doubling the population size equals to the increase by 200%, while reducing the population to one half equals to the decline by 50%. These incomparable values make inference from interspecific comparisons of such trends impossible (Lemoine et al., 2007). Therefore, we followed Lemoine et al. (2007) and recalculated the population change using the expression $(N_{t+1} - N_t) / ((N_{t+1} + N_t)/2)$, when N_t is population size in the time t (i.e. 2000) and N_{t+1} is population size in the time $t + 1$ (i.e. 2012). N_t was set to 100% and N_{t+1} was the relative population change proportional to the original trend value (e.g. for the population decline by -20%, the $N_{t+1} = 80\%$; for the population increase by 20%, the $N_{t+1} = 120\%$). By that means, we obtained an index of population change ranging from -2 to 2, when negative values correspond to population declines, positive values to population increases and zero to no change. Values of this index are symmetrical for population declines and increase (for instance, doubling the population size equals to the index value of 0.67, while reducing the population size to one half equals to the index value of -0.67). This population index was thus taken as a response variable for further analysis.

2.2. Annex I species and country classification

To focus on testing the efficiency of listing the species under the Annex I of the Birds Directive, we discriminated the species being listed (1) from those being unlisted (0) according to the information in BirdLife International (2015), see Supplementary Table S.1. Since we expected country-specific effects of being listed on species’ population trend varying according to the time a given country entered EU, we classified the countries as the old member states (i.e. countries which entered EU before 2004), the new member states (i.e. the countries which entered EU from 2004 onwards) and non-member states (i.e. the countries which did not access EU). This classification was expressed as a three-level factor ‘country status’ (Supplementary Table S.2) and was used as a country-specific explanatory variable for further analysis.

2.3. Species’ traits

For each species, we collected information about the following 11 traits (see Table 1 for summary information and Supplementary Table S.1 for trait values for each species).

Habitat use was expressed using four variables taken from Koschová et al. (2014). Each species was assigned to one of more habitats along a gradient from forest interior (position of 1) to open treeless landscape (position of 7) assessed in Böhning-Gaese and Oberrath (2003). From this assignment (i) habitat niche position was calculated as the mean value of across habitats used by a given species (Reif et al., 2011). As a complement to the habitat niche position, (ii) habitat niche breadth was

Table 1

Characterization (a) and predicted relationships to population trends (b) of the traits considered for the analysis of European bird population trends.

a)		
trait ID	trait name	description
1	habitat niche position	mean of species' positions along the gradient from closed forest (1) to open treeless habitat (7)
2	habitat niche breadth	range of species' positions along the gradient from closed forest (1) to open treeless habitat (7)
3	position along the humidity gradient	species' positions along the gradient from non-humid (1) to water habitat (3)
4	relation to built-up areas	discrimination among species breeding (1) and not breeding (0) in built-up areas
5	mean latitude of breeding range	latitude of the centre of species' breeding range in Europe (in decimal degrees)
6	potential range shift	magnitude of the shift of the range centre between the current and the predicted future breeding range in Europe (in km)
7	diet niche breadth	(1) obligatory herbivorous or insectivorous/carnivorous, (2) herbivorous and insectivorous/carnivorous, (3) omnivorous
8	migratory strategy	(1) residents, (2) short-distance and (3) long-distance migrants
9	marginality of European distribution	distance between the centre of the species' European and Eurosian breeding range (in decimal degrees)
10	life history strategy	position along the slow-fast life history gradient revealed by a principal component analysis on six species' life-history traits
11	nest location	species breeding on or near ground (0), in shrubs and small trees (1), in high trees (2)

b)			
trait ID	predicted relationship	mechanism	reference
1	more negative trends in species more associated with open habitats	agricultural intensification, forest encroachment on open habitats	Butler et al. (2010)
2	more negative trends in more specialized species	higher sensitivity of habitat specialists to environmental change	Le Viol et al. (2012)
3	more negative trends in species more associated with more humid habitats	destruction of wetlands, eutrophication, decrease in ground water level	Lehikoinen et al. (2016)
4	more positive trends in species more associated with built-up areas	exploitation of free ecological space after urbanization	Evans et al. (2011)
5	more negative trends in species breeding at higher latitudes	detrimental impact of climate change on cold-adapted species	Stephens et al. (2016)
6	more negative trends in species with lower temperature resilience	detrimental impact of climate change on climatic specialists	Jiguet et al. (2006)
7	more negative trends in diet specialists	higher sensitivity of diet specialists to environmental change	Van Turnhout et al. (2010)
8	more negative trends in species with longer migration distance	environmental changes on wintering grounds, climate change, higher sensitivity of migrants	Finch et al. (2017)
9	more negative trends in species with populations further from range centre	less efficient buffer to environmental perturbations in marginal populations	Diaz et al. (2015)
10	more negative trends in species with slower life history strategies	lower resilience of species with low pace of life to environmental perturbations	Owens and Bennett (2000)
11	more negative trends in species with nests located closer to ground	higher exposure of ground nesting species to the increased nest predation risk	Chalfoun et al. (2002)

expressed as the difference between the values of habitats used by a given species at the extremes of the gradient mentioned above (Reif et al., 2011). Classification of species' position along the (iii) humidity gradient discriminated species of non-humid (1), wetland (2) and water habitats (3) assessed in Böhning-Gaese and Oberrath (2003). Finally, we assessed (iv) species' relation to built-up areas discriminating species breeding in such areas (1) and species not breeding in these areas (0) using information in Cramp (1977–1994).

The effects of climate change were expressed using two variables taken from Koschová et al. (2014) based on characteristics of European breeding ranges of particular species: (i) latitude of the mean range centre and (ii) magnitude of potential range shift. Koschová et al. (2014) used maps from Huntley et al. (2007) for their inference. These maps were constructed using bioclimatic modelling of the breeding bird distribution in Europe using the information from Hagemeijer and Blair (1997) on current breeding ranges of particular species. Huntley et al. (2007) first modelled the present climatic range of every species and the revealed relationship between species' breeding distribution and climatic variables was applied in the next step to predict the future climatic ranges of bird species under the climatic projection for the period 2070–2099 (IPCC, 2001). Using these data from Huntley et al. (2007), Koschová et al. (2014) calculated the mean centre (mean longitude and mean latitude), for both the current and the predicted future climatic range of every species. The potential range shift of a given species was the difference between these mean centres in kilometres (Koschová et al., 2014).

We also considered five more ecological traits to test their potential relationships to bird population trends: (i) diet niche breadth was based on a classification of species into three groups: obligatory herbivorous

or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2) and omnivorous (3) in Koschová et al. (2014); (ii) migration strategy was based on classification of species as residents (1), short-distance migrants (2), and long-distance migrants (3) in Koschová et al. (2014); (iii) marginality of the position of species' European breeding ranges in respect to their Eurasian breeding ranges (expressing the marginality of the European distributions) was calculated as a distance between mid-longitudes of Eurasian and European ranges based on the analysis of range maps from BirdLife International (2016) – the larger the difference, the more marginal population is represented by our European data for a given species; (iv) life history strategy was taken from Koschová et al. (2014) who expressed position of each species along a slow-fast life history axis revealed by principal component analysis of six life-history traits: body mass, egg mass, number of broods per year, laying date (julian date of the beginning of laying in the first breeding), clutch size and length of incubation; (v) nest location was based on data from Koleček et al. (2014) who recognized species breeding on the ground or close to (0), species breeding in intermediate heights such as shrubs and small trees (1) and species breeding in high trees (2).

We tested for possible collinearity among the trait variables by calculating the Pearson correlation coefficients for each pair of variables (Supplementary Table S.3) and found that all correlations were below 0.7 which is considered as a level when the issue of collinearity arises (Dormann et al., 2013).

2.4. Data analysis

We used linear mixed effects modelling framework within the R

package ‘nlme’ (Pinheiro et al., 2010) to test the influence of listing under the Annex I of the Birds Directive on population trends of European birds. We proceeded in several steps following the approach of Koleček et al. (2014) who performed a similar analyses focused on the efficiency of the national legislation for protection of bird species in ten Eastern European countries. First, we selected the species’ traits with the largest continent-level influence on bird population trends to control for their possible confounding effects on population trends potentially masking the effect of the Annex I of the Birds Directive. For this purpose, we run the models with the main effects of particular species’ traits and the interaction between the potential range shift and the latitude of the mean range centre to account for variability in climate change impacts on species across latitudes (see Koschová and Reif, 2014). We performed model selection based on the information-theoretic approach to assess the relative importance of all possible combinations of the predictor variables (Burnham and Anderson, 2002). Using Akaike Information Criterion corrected for small sample sizes (AIC_c) we assessed relative performance of every combination of predictor variables within the R-package ‘MuMin’ (Barton, 2015) and selected the models with ΔAIC_c less than two as the best performing models (Burnham and Anderson, 2002). Second, we took the variables present in these best performing models and composed a final model where we added the variable ‘listing the species under the Annex I’, the variable ‘country status’ and their interaction. This interaction tests for the differences in the effect of listing the species under the Annex I among the old member states, the new member states and the non-member states. We assessed the importance of this interaction using the likelihood ratio test. To take the replicates at the species- and country-level into account, we included the variable ‘species’ nested within the variable ‘country’ as random effects into all models following the approach of Gamero et al. (2017). All analyses were performed in R 2.12.0.

3. Results

In the analysis selecting the species’ traits according to the strength of their relationships to population trends, three models were assessed as the best performing ones by the information-theoretic approach with their ΔAIC_c lower than two (Table 2). All these models contained nest location and life history strategy, two models contained species’ position along the humidity gradient and one model contained habitat niche breadth (Table 2).

In the next step, we combined these variables into a single model, where we also included listing the species’ under the Annex I of the Birds Directive, country status and their interaction (Table 3). This interaction was found as significantly improving the model fit according to the likelihood ratio test (likelihood ratio between the models with and without this interaction = 9.90, $P = 0.007$), so we used this model as the final one for the inference.

The parameter estimates of this final model (Table 3) showed that listing the species under the Annex I resulted in significantly increasing population trends and that this improvement of populations in the listed species was highest in the old member states (Fig. 1). For the new member states, the positive effect of listing the species under the

Table 2

Characteristics of the best performing linear mixed-effects models relating population trends to species’ traits of European birds. Model performance was assessed by Akaike information criterion (AIC_c) across all possible combinations of the trait variables and the best performing models are those with $\Delta AIC_c < 2$. See Table 1a for variable identification.

model terms	no of parameters	AIC_c	ΔAIC_c	model weight
10 + 11	6	5440.00	0.00	0.43
3 + 10 + 11	7	5441.59	0.59	0.32
2 + 3 + 10 + 11	8	5441.11	0.11	0.25

Table 3

Relationships between population trends of European birds and listing the species under the Annex I of the Birds Directive in old European union’s member states (i.e. those entered EU before 2004), new European union’s member states (entered EU from 2004 onwards) and non-member states, respectively, estimated by the final linear mixed-effects model taking into account the effects of the species’ traits previously selected as important by the information theoretic approach (see Table 2). Significant results are in bold.

model term	coefficient	SE	df	t	P
habitat niche breadth	0.015	0.004	4420	3.32	0.001
position along a humidity gradient	0.043	0.011	4420	4.02	< 0.001
life history strategy	-0.016	0.004	4420	-3.50	0.001
nest location	0.050	0.009	4420	5.67	< 0.001
EU non-member states	-0.188	0.041	30	-4.63	< 0.001
EU new member states	-0.180	0.039	30	-4.57	< 0.001
EU old member states	-0.195	0.037	30	-5.21	< 0.001
annex I in EU non-member states	-0.009	0.028	4420	-0.33	0.741
annex I in EU new member states	0.071	0.028	4420	2.53	0.012
annex I in EU old member states	0.105	0.025	4420	4.21	< 0.001

Annex I was slightly lower but still significant (Fig. 1), while no significant relationship between population trend and listing under the Annex I was observed in the non-member states (Fig. 1).

All trait variables included into the final model were significantly related to bird population trends (Table 3). More positive trends were found for species having broader habitat niches, breeding in more humid habitats, having slower life history strategies and breeding higher above ground (Table 3).

4. Discussion

Our results showed that listing the species under the Annex I of the EU’s Birds Directive resulted in their more positive population trends compared to the non-listed species. Importantly, this positive effect of legal protection was not confined only to the so called old member states of EU (i.e. the countries which entered EU before 2004) reported by Donald et al. (2007) and Sanderson et al. (2016), but were also observed for the new member states, i.e. the countries entering EU from 2004 onwards. Our study thus for the first time showed significant conservation benefits delivered by listing the species’ under the Annex I applies to the whole EU. These positive effects of EU’s conservation legislation contrast with their absence in the countries which are not EU members.

What is the mechanism mediating the population benefits for birds being listed under the Annex I of the Birds Directive in EU countries? We suggest three important drivers of this success: (i) setting the EU-wide (i.e. supranational) conservation priorities, (ii) scientific basis of species selection and (iii) establishment of protected areas for the species. Concerning the first point, it is important to realize that the bird species’ ranges are usually much larger than the areas of individual countries (Gaston, 2003) and that species’ populations are connected by dispersal or migration among countries (Gilroy et al., 2016). Therefore, protection of a species in one country may be effectively compromised by its absence for the same species in a neighbouring state (Pouzols et al., 2014). The Birds Directive overcomes this problem by protecting the species’ populations from the EU-wide perspective. By that means, the species recognized as deserving protection in EU are listed under the Annex I in all member states which results in protection of significant parts of their European (or even global) populations. This large-scale protection may then translate in population increase in all countries involved.

Second, species are selected for Annex I within a sophisticated system of scientific criteria. They focus on species’ population status in EU and on the proportion of EU’s population shared by individual countries (Donald et al., 2007). By that means, a country protects the

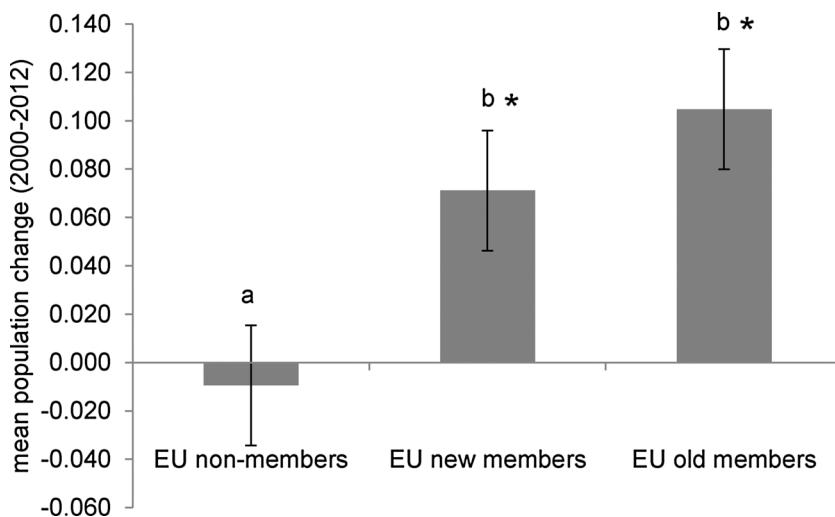


Fig. 1. Relationships between population trends of European birds and listing the species under the Annex I of the Birds Directive in old European union's member states (i.e. those entered EU before 2004), new European union's member states (entered EU from 2004 onwards) and non-member states, respectively, estimated by the final linear mixed-effects model. The effects of the species' traits potentially affecting bird population trends were controlled for (Table 3). The respective bars depict the effect of listing under the Annex I estimated by the model for respective groups with \pm standard error. Different letters above bars indicate statistically significant differences between respective groups. Astrisk above bars indicates statistically significant differences from zero.

species of the EU-wide interest whose significant part of population occurs in that country (Donald et al., 2007). This guarantees efficient spending of inevitably limited conservation resources when the greatest emphasis is targeted to areas hosting the population strongholds of the focal species, whereas marginal areas where a given species occurs rarely are neglected. This approach is in accord with the current knowledge of population ecology of animals in space showing that source populations are crucial for species' persistence, while sinks are of minor importance (Pulliam, 1988). Third, although the sole effect of listing as legally protected may be beneficial for the target species in terms of the reduction of the direct persecution (Koleček et al., 2014), the species listed under the Annex I enjoy particular benefits from establishment of protected areas, i.e. SPAs, aimed specifically to satisfy the local needs of these species (Donald et al., 2007). Designation of individual SPAs is performed at the national level by local experts based on scientific criteria to cover the key localities for species' population in a given country (Donald et al., 2007). Once again, this approach ensures that the focal species are protected at their most important sites of occurrence from the EU-wide perspective.

Our study supports the findings of Sanderson et al. (2016) about longitudinal increase of positive effect of listing the species under the Annex I. We found that the listed species had the most positive trends in the old member states and somewhat less positive in the new member states, but the difference between old and new member states was not significant. As the usual time lag between listing the species as protected and detection of improvement of its population status is between 5 and 10 years (Male and Bean, 2005; Sanderson et al., 2016), we suggest that this result broadly coincides with the start of EU-membership in the majority of the new member states in our sample which took place in 2004. Therefore, the time period of 2000–2012 used for the estimation of the abundance trends most likely mirrors population improvement of the listed species in new member states after their EU entrance and the pattern was probably not caused by some other factors. Our results thus imply that even if the new member states underwent historical development largely different from the old member states (Reif et al., 2011), implementation of the EU's conservation legislation was successful in these countries and resulted in conservation benefits for the Annex I species. We can predict that the population improvement of these species in the new member states will be even stronger in the future with the longer time elapsed since their EU entrance. Another concern about the observed positive influence of EU's conservation legislation may be that the bird populations in the new member states may improve even without entering EU due to generally better environmental conditions in the Eastern European countries, which are believed as strongholds of European biodiversity (Sutcliffe et al., 2015). However, a great contrast in the statistical effect of the

species' listing between the new member states and non-members indicates that this mechanism is hardly applicable. In addition, we did not observe any differences in mean bird population trends (after controlling the effect of listing) among old member states, new member states and non-members implying that presumably better environmental conditions in the Eastern Europe either recently deteriorated or did not mirror in positive bird population trends.

Recognition of species' threat based on an unfavourable population status is a usual first step before including a given species among those that are legally protected (Sutherland, 2000). For this purpose, the IUCN Red List is the most widely used and respected tool under which the species are assessed based on purely biological criteria concerning population and geographic range size characteristics (Mace et al., 2008). However, listing the species under the IUCN Red List (either global or regional) does not guarantee that this species will be inevitably the subject of a conservation management including its listing among legally protected species. Indeed, an assessment of the rates of species' movement between particular IUCN Red List categories among assessments performed at different time points indicates that only the most threatened species move more often towards downlisting than towards uplisting in the subsequent assessment, while the less threatened species are more often uplisted (Brooke et al., 2008). This is in a clear contrast to our finding that the species listed as protected in EU have population trends more positive than the unprotected species. It thus seems that the way from recognition of a species as threatened to a detectable improvement of its population status is quite long and the success at the end is uncertain. Therefore, we suggest that the links between threat assessments and listing the species as protected should be closer and the EU's conservation legislation may be inspirational in this respect.

Our results add to the evidence that listing the species as protected by law is beneficial for their population growth corresponding to several other studies showing population increases of legally protected species in different parts of the world (Male and Bean, 2005; Vorisek et al., 2008; Koleček et al., 2014; Gamero et al., 2017). This may be a positive message for conservationists involved in creation of protected species lists because it shows general efficiency of this effort. However, global applicability of the findings of these studies is still not inevitable for two reasons. First, all of these studies are confined to the North America and Europe, i.e. the richest and the most developed regions of the world. It is well known that people's awareness of environmental issues followed by development of efficient solutions is often associated with obtaining a given level of economy (Dinda, 2004), as depicts the Kuznets curve which has been shown applicable also for bird populations (Lantz and Martínez-Espíñeira, 2008). Therefore, it is possible that the conditions in the North America and Europe are simply more

suitable for a higher efficiency of conservation legislation in terms of scientific basis and enforcement than elsewhere. Second, the reports of positive effects of legal protection on bird populations may be easier to publish in relevant journals than the findings of insignificant or even negative effects, which may produce a publication bias (Fanelli, 2012). Therefore, the overview based on the existing studies may be perhaps too optimistic and further assessments, especially from regions other than the North America and Europe, are needed to make general conclusions about the positive effects of being listed as procted.

Our analysis controlled for the influence of a comprehensive set traits recently being recognized as important correlated of bird population trends (Reif, 2013). We found that following four of these traits were significantly related to the trends together with the effect of listing under the Annex I: habitat specialization, position along the habitat humidity gradient, life history strategy and nest location. These results confirmed the previous findings of continent-wide decline of habitat specialists leading to homogenization of bird communities (Le Viol et al., 2012), which is probably caused by higher sensitivity of more specialized species to various human-induced environmental impacts which recently magnify (Devictor et al., 2008), whereas habitat generalists are more resilient and they can even benefit from the new opportunities provided by altered habitats (Hanzelka and Reif, 2015). In contrast, the observed population increase of the species associated with wetlands was rather unexpected (compare with Lehikoinen et al., 2016), but corresponds to recent observations of population increases of wetland birds in several European countries such as the Netherlands (Van Turnhout et al., 2007) or the Czech Republic (Koleček et al., 2010) which may be attributable to the increased conservation effort aimed to wetland habitats and population expansion of many waterbird species following the climatic amelioration (Musil et al., 2011). We also did not expect more negative trends in species with faster life history strategies since those should be more resilient to environmental perturbations due to their high reproductive potential (Owens and Bennett, 2000). However, it seems that the recent global change conditions may indeed favour the species with slower life history strategies due to their ability to wait for longer time until the conditions are more suitable for reproduction, whereas the species with faster strategies (associated with shorter life span) are forced to reproduce under suboptimal conditions (Sol et al., 2012) leading to their population decline. Similar results were recently found in studies focusing on population of French (Jiguet et al., 2007) and Eastern European birds (Koleček et al., 2014). Finally, we found some evidence that species breeding closer to the ground have declined, supporting the findings of several other studies on European birds (Gregory et al., 2007; Van Turnhout et al., 2010; Koleček et al., 2014). This pattern may mirror continuation of the negative impacts of human land use in open habitats (e.g. agricultural intensification) where the majority of such species breed (Butler et al., 2010), but may be also attributable to the increased predation pressure from the side of recently introduced predators (Chalfoun et al., 2002).

In conclusion, our study showed a positive influence of listing the species under the Annex I of the Birds Directive on their populations in the EU member states in contrast to the non-members. As birds are often taken as indicators for other groups of organisms with less complete data on their population abundance (Westgate et al., 2016), we can speculate whether or not the conservation benefits delivered by the EU's conservation legislation may apply also to the other ecosystem components. Despite some indications that this might be the case for specific groups of organisms in several countries (e.g. Cantarello and Newton, 2008; Lison et al., 2013, 2015), some other studies report the opposite results (Diserens et al., 2017). Therefore, a need for a continent-wide assessment similar to the one presented in this study for birds, should be one of the priorities of conservation science (see also Hermoso et al., 2017).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.11.019>.

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